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Low Frequency of Stabilimenta in Orb Webs of *Argiope appensa* (Araneae: Araneidae) from Guam: An Indirect Effect of an Introduced Avian Predator?[1]

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ABSTRACT: The occurrence and patterns of stabilimenta in 1195 webs of the orb weaver *Argiope appensa* (Walckenaer) from four islands in the Mariana Archipelago were recorded. Webs on the largest and southernmost island, Guam, had significantly fewer stabilimenta (16.4%, $n = 359$) than webs of conspecifics from the neighboring islands of Rota (56.9%, $n = 211$), Tinian (41.9%, $n = 315$), and Saipan (50.3%, $n = 310$), as well as from webs of *Argiope* spp. worldwide (47.8%, $n = 5662$). The differences in stabilimentum frequency in webs between sites in the Marianas were not correlated with vegetation, light levels, the distribution of individuals within web size classes, or the presence of certain stabilimentum patterns. Factors operating at scales smaller than the sample sites may influence stabilimentum frequency, because several locations showed nonrandom clumping of decorated webs. One theory for the function of stabilimenta is that they reduce damage to the web by warning flying birds of the web's location. Because Guam's native birds have been eliminated recently by the introduction of the brown tree snake, *Boiga irregularis* (Merrem), the low frequency of decorated webs of *A. appensa* on Guam might, therefore, be either a behavioral response to the avian extinctions or a result of reduced selection for stabilimenta in the absence of birds.

WEB DECORATIONS, often called stabilimenta, are the distinct bands or spirals of white silk found in the center of the webs of certain diurnal orb-weaving spiders, such as members of the families Araneidae and Uloboridae. Several hypotheses have been advanced to explain the function of stabilimenta, but only two theories have experimental support: (1) The highly visible structures may be warning devices to prevent birds from inadvertently flying into and destroying the webs (Horton 1980, Eisner and Nowicki 1983); (2) Because stabilimenta reflect ultraviolet light, and thereby attract insects to a web, the structures may serve as prey attractants (Craig and Bernard 1990, Craig 1991).

Several untested functions of web decorations have also been proposed. The character may help defend against predators either by distorting a spider's shape and making it appear much larger than it is (Edmunds 1986, Eberhard 1990) or by camouflaging the spider (Hingston 1927, Marson 1947, Ewer 1972, Eberhard 1973, Tolbert 1975, Eberhard 1990). Stabilimenta may stabilize a web (Robinson and Robinson 1973) or reinforce a web so that it forms a shield against predators (Robinson and Robinson 1970, Tolbert 1975). A stabilimentum may be a hormonal reaction to stress or have no function (Nentwig and Rogg 1988). Because no hypothesis accounts for all web-decoration attributes, several authors (Eberhard 1973, Tolbert 1975, Nentwig and Heimer 1987, Robinson 1987) have suggested that stabilimenta may serve more than one function, either simultaneously or at different stages in a spider's development.

The occurrence and patterns of stabilimenta may vary within a species according to a spider's size and age (Ewer 1972, Lubin 1975, Tolbert 1975), readiness to molt (Nentwig and Heimer 1987), the presence of male spiders in a female's web (Nentwig and Rogg 1988), and

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proximity to other orb-web weaving spiders (Craig 1991), as well as according to temperature extremes (Nentwig and Rogg 1988) and light levels (Marson 1947, Eberhard 1973). Initial observations suggested that on Guam, an oceanic island in the western Pacific, *Argiope appensa* (Walckenaer) webs had fewer stabilimenta than webs of conspecifics on neighboring islands. I censused webs on Guam and three adjacent islands, Rota, Tinian, and Saipan, to determine how stabilimentum frequency varied between islands. Specifically I asked the questions: (1) Are the differences in web-decoration frequencies between islands correlated with web size or habitat features such as vegetation and level of insolation? (2) Can stabilimentum frequency change at a site over time? (3) Are decorated webs dispersed randomly among a population at a site?

METHODS

Study Sites and Organism

Argiope appensa is an orb-weaving spider in the family Araneidae and has been recorded from Australia and New Caledonia to Hawaii (Suman 1964). *Argiope appensa* is the dominant species of *Argiope* in Micronesia and the only species of the genus reported from the southern Marianas (Levi 1983). Body length of adult females is about 20 to 25 mm. Unlike some *Argiope*, which change stabilimentum form with age (Ewer 1972), both juveniles and adults of *A. appensa* build X-shaped stabilimenta. The stabilimentum may consist of any combination of the four arms (the complete cruciate pattern is only rarely made) or the structure may not be built at all. During the rainy season from June to November, *A. appensa* is a common inhabitant of sunny "edge" areas, such as along roadsides, cultivated areas, strand habitats, stream banks, and forest gaps in the Mariana Islands. It is much less numerous in the understory of native ravine and limestone forests.

From May 1990 to June 1992, field observations on webs of *A. appensa* were made on four neighboring volcanic and uplifted limestone islands in the southern Mariana Archipelago: Guam (13° N, 145° 42′ E, 540 km^2), Rota (14° 10′ N, 145° 39′ E, 85 km^2), Tinian (15° N, 145° 38′ E, 102 km^2), and Saipan (15° 12′ N, 145° 37′ E, 140 km^2). The names of the sampled sites were taken from U.S. Geological Survey topographic maps, with the exception of Laolao, which consisted of two adjacent beaches, Unai Laolao and Unai Bapot. Complete descriptions of the vegetation of these sampled islands are found in Fosberg (1960) and Stone (1970).

Six areas were surveyed for webs on Guam: Mangilao, Pago, Talofofo, Urunao, Yigo, and Ylig. Five areas were sampled on Rota: Applatatgua, As Mundo, Esong, Gigani, and I Batko. On Tinian I censused three sites: Bateha, Mangpang, and West Field; and on Saipan I surveyed two locations: Laolao and Obyan.

Field Observations

For each site, the occurrence and patterns of stabilimenta were recorded for all webs seen within 0.5 to 2 h. While facing the superior plane of the nearly vertical webs, I recorded the number of stabilimentum arms, their positions, and whether they passed through the web's center. Web area for the Guamanian (Mangilao and Pago) and Rotanese (Applatatgua, As Mundo, and Esong) samples taken in 1990 was computed as an ellipse using horizontal and vertical web diameters measured between the outermost spiral strands. Web-area distributions of orb-web weaving spiders approximate body-length distributions (Reed et al. 1969, Lubin 1975, Leborgne and Pasquet 1986) and were used to correlate spider age with stabilimentum frequencies. Abandoned, damaged, or abnormal webs such as those made by spiders missing legs or webs containing dead spiders were not included in statistical analyses.

The dominant plants at each site were noted and vegetation communities were classified according to Fosberg (1960) and Stone (1970). Light levels were assigned qualitatively: Webs were categorized as sunlit if they received sunlight for at least part of the day (e.g., most webs along roadsides or in the strand). Shaded webs were those in areas, such as under dense

vegetation and rock overhangs, that received no direct sunlight. To determine if stabilimentum frequency for a site changed over time, I resurveyed webs at Laolao (Saipan), Esong (Rota), Talofofo (Guam), and Mangilao (Guam) 2 months, 24 months, 12 months, and 8 months, respectively, after the first censuses.

Statistical Analyses

I used a one-way analysis of variance (ANOVA) to see if stabilimentum frequency or web size distributions differed between islands. To ensure that a spider was sampled only once, I randomly excluded webs from one of the censuses from Laolao, which were taken only 2 months apart. Tukey's honestly significant difference pairwise comparison of means (Sokal and Rohlf 1981) was used to find differences among island means. Differences in stabilimentum frequency in web size classes between Guam and Rota were examined with a two-way ANOVA without replication using islands and web size as factors. Frequencies in the parametric procedures were arcsine-squareroot transformed and homogeneity of variance was checked with an F_{max} test before analysis.

Because of smaller sample sizes, the effects of vegetation (site), time, and light levels were examined as presence or absence of stabilimenta via 2×2 G tests with Williams' correction for small sample size (Sokal and Rohlf 1981). Sites generally were characterized by only one plant community. Therefore, to check for effects of vegetation, I examined site homogeneity by making all pairwise comparisons within each island. To examine the effect of light levels, webs were pooled within islands into shaded and unshaded categories, and data for each island were examined sepa-

TABLE 1

PERCENTAGE OF STABILIMENTA IN *Argiope appensa* WEBS FROM THE MARIANA ISLANDS

				WEB LOCATION					
ISLAND	SITE	VEGETATION	DATE	SUN	*n*	SHADE	*n*	COMBINED	*n*
Guam	Mangilao	Limestone	30 May 1990	11.1	19	23.5	51	20.3	70
		Disturbed	14 Jan. 1992	11.1	18	33.3	3	14.3	21
	Pago	Strand	29 May 1990	0.0	4	29.3	41	26.7	45
	Talofofo	Limestone	23 June 1990	ND	0	8.3	36	8.3	36
		Limestone	16 June 1991	0.0	1	3.7	27	3.6	28
	Urunao	Limestone/Backstrand	26 June 1990	21.4	14	18.2	66	18.8	80
	Yigo	Limestone/Disturbed	07 Aug. 1990	16.0	50	0.0	2	15.4	52
	Ylig	Limestone	14 Mar. 1992	18.2	11	6.3	16	11.0	27
	Combined sites			14.5	117	17.4	242	16.4	359
Rota	Applatatgua	Limestone/Disturbed	26 May 1990	18.2	11	37.0	27	31.6	38
	As Mundo	Limestone	26 May 1990	60.0	15	33.3	3	55.6	18
	Esong	Disturbed	28 May 1990	44.7	47	60.0	5	47.1	52
		Disturbed	01 June 1992	71.0	62	100.0	1	71.4	63
	Gigani	Limestone/Disturbed	26 May 1992	66.7	15	ND	0	66.7	15
	I Batko	Strand	31 May 1992	87.5	8	70.6	17	76.0	25
	Combined sites			58.9	158	50.9	53	56.9	211
Tinian	Bateha	Disturbed	15 June 1990	47.9	165	ND	0	47.9	165
	Mangpang	Disturbed	15 June 1990	28.4	81	ND	0	28.4	81
	West Field	Disturbed	15 June 1990	43.8	69	ND	0	43.8	69
	Combined sites			41.9	315	ND	0	41.9	315
Saipan	Laolao	Strand	05 Oct. 1991	46.0	113	14.3	14	42.5	127
		Strand	27 Aug. 1991	69.8	53	88.0	25	75.6	78
	Obyan	Strand	05 Sept. 1991	41.0	105	ND	0	41.0	105
	Combined sites			48.7	271	61.5	39	50.3	310
Combined islands				43.4	861	27.8	334	39.1	1,195

NOTE: *n*, sample size; ND, no data.

rately. For time effects, samples from the first and second surveys were examined for each site. Between-island differences in stabilimenta patterns were tested with an $R \times C$ test of independence using the G statistic (Sokal and Rohlf 1981). For nonorthogonal pairwise comparisons within islands, significance levels were adjusted using $\alpha' = 1 - (1 - \alpha)^{1/k}$, where α' is the adjusted level of significance, k is the number of comparisons, and α is the unadjusted significance level in this study (0.05) (Sokal and Rohlf 1981).

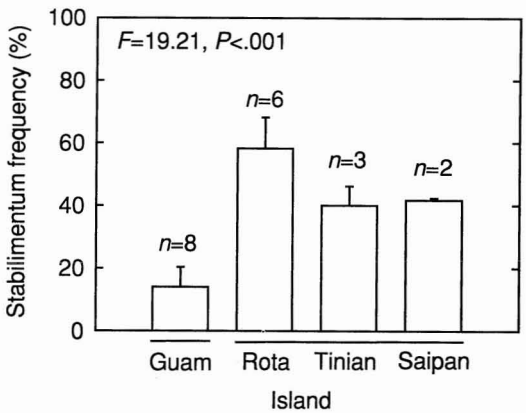

FIGURE 1. Frequency of stabilimenta in webs from the Mariana Islands. Data are backtransformed means and standard deviations. Lines below bars indicate homogenous sample means; n, sample size.

Argiope appensa webs were often concentrated along ecotones (strand-beach, roadside-forest, or fencerows) and positioned between 1 and 2 m above the ground. Therefore, in essentially one-dimensional habitats such as these, I checked for nonrandom clumping of decorated webs with a normal approximation of a runs test for dichotomized data (Sokal and Rohlf 1981).

RESULTS

The frequency of stabilimenta in 1195 webs from the sampled islands is shown in Table 1. The frequency of stabilimenta in webs from all islands combined was 39.1%. Webs on Guam had significantly fewer stabilimenta

TABLE 2

FREQUENCY OF STABILIMENTA IN *Argiope* SPP. WEBS WORLDWIDE

SPECIES	WEBS WITH STABILIMENTA (%)	n	STUDY SITE	REFERENCE
Argiope aemula (Walckenaer)	91.6	83	New Guinea	Robinson and Robinson (1974)
A. appensa (Walckenaer)	16.4	359	Guam, Marianas	This study
	56.9	211	Rota, Marianas	This study
	41.9	315	Tinian, Marianas	This study
	50.3	310	Saipan, Marianas	This study
A. argentata (Fabricius)	34.5	2,614	Panama	Robinson and Robinson (1970)
	75.4	65	Jamaica	Marples (1969)
	24.5	141	Daphne Major, Galápagos	Lubin (1975)
	41.8	134	Santa Cruz, Galápagos	Lubin (1975)
A. bruennichi (Scopoli)	67.8	90	France	Marples (1935)
A. lobata (Pallas)	74.6	63	France	Marples (1969)
A. picta L. Koch	46.8	400	New Guinea	Robinson and Robinson (1974)
A. pulchella Thorell	≥68.3*	60	Burma	Marson (1974)
A. reinwardti (Doleschall)	78.5	65	New Guinea	Robinson and Robinson (1974)
A. trifasciata (Forskål)	46.0	752	Ghana	Edmunds (1986)
Combined species	≥47.8	5,662		

NOTE: n, sample size.
* Data given as lower limits.

than webs from the other sampled islands (Figure 1) and had the lowest frequency for *Argiope* spp. webs worldwide (Table 2). Habitat appeared to have a negligible effect on stabilimentum frequency; only five of 49 pairwise comparisons of sites were significantly different (Table 3). Three of these significant comparisons involved webs from pairs of sites with the same vegetation (Table 1). Light levels seemed not to consistently affect web form, either: Of webs from the three islands (Guam, Rota, and Saipan) having samples of both shaded and unshaded webs, only those from Saipan showed a significant within-island difference between stabilimentum frequencies in sunny and shaded areas ($G = 13.50$, $P < 0.01$).

The frequency of stabilimenta did not significantly increase with web area on Guam and Rota (Figure 2A). The web size distributions from Guam and Rota also did not differ significantly (Figure 2B). Webs from Guam had lower frequencies of stabilimenta in each size class than those from Rota. A significant difference between sampling dates occurred in webs at Laolao, Saipan (Table 3). Conversely, the frequency of stabilimenta in webs at Talofofo, Guam, remained steady for 1 yr (Table 3).

The proportions of stabilimentum patterns varied significantly between islands ($G = 37.15$; df = 9; $P \ll 0.001$) (Table 4). Tinian webs had the highest proportion of diagonals (91.5% of the decorated webs) of any Mariana Island; Saipanese webs had a large number of crosses (8.8%) and "other" forms (11.8%), mostly aberrant designs and those with single upper elements. Diagonals were the most frequently observed pattern in the Marianas (76.8% of the decorated webs), whereas λ-shaped and abnormal stabilimenta occurred least often in the archipelago (both $<0.01\%$). Nonrandom clumping of webs occurred at three of five sites: Esong (first survey), Rota ($n = 35$, runs [R] = 12, $P = 0.020$); Pago, Guam ($n = 43$, R = 11, $P = 0.008$); and Obyan, Saipan ($n = 111$, R = 32, $P < 0.001$). Stabilimenta were randomly distributed among webs at Mangpang, Tinian ($n = 71$, R = 32, $P = 0.488$), and Yigo, Guam ($n = 44$, R = 15, $P = 0.480$).

Most abnormal stabilimenta had extra arms or arms arranged at peculiar angles (e.g., equilaterally tripartite). However, one very unusual stabilimentum was observed. At Banzai Cliff, Saipan, the web of an adult female had a thick, parchment-like, discoid stabilimentum about 3 cm across (author's photo record). On all islands, small juveniles made stabilimenta with proportionately larger and thicker arms than older spiders. Stabilimenta in Tinian webs seemed to be made with less silk, often appearing fainter than those from other islands.

DISCUSSION

Webs of *Argiope appensa* on Guam had the lowest incidence of stabilimenta ever recorded. Webs of congeners worldwide often have stabilimenta two to five times more often than Guamanian *A. appensa* (Table 2). Webs of conspecifics from neighboring islands also had significantly higher frequencies of decorations than did *A. appensa* from Guam (Fig. 1).

Older *Argiope* spiders may decorate their webs more often than juveniles (Lubin 1975, but see Nentwig and Rogg 1988). Guam had lower proportions of decorated webs in each size class (Figure 2A), suggesting that differences in age distributions between the islands did not account for the low frequency of decorated webs on Guam. However, *Argiope* build progressively smaller webs after the last instar (Reed et al. 1969), which may have inflated the decoration frequencies of the two smaller size classes from Rota. Nevertheless, in the largest web size category, the category best controlling for possible age differences, Guamanian webs still had fewer stabilimenta than Rotanese webs (Figure 2A).

Stabilimentum frequencies of webs of Mariana Island *A. appensa* were probably not influenced by habitat features. *Argiope* may build more stabilimenta in well-lit areas (Marson 1947). However, other studies have failed to find a consistent correlation between light intensity and stabilimentum frequency (Edmunds 1986, Nentwig and Rogg 1988). Differences in stabilimentum frequencies between sunny and shaded webs in the Mariana

TABLE 3

G STATISTIC SUMMARY MATRIX OF PAIRWISE BETWEEN-SITE COMPARISONS OF STABILIMENTUM FREQUENCIES

	MANGILAO1	MANGILAO2	PAGO	TALOFOFO1	TALOFOFO2	URUNAO	YIGO	YLIG	APPLAT	AS MUNDO	ESONG1	ESONG2	GIGANI	I BATKO	BATEHA	MANGPANG	WEST FIELD	LAOLAO1	LAOLAO2	OBYAN
Obyan																		22.23*	0.06	—
Laolao2																		21.92*	—	
Laolao1																		—		
West Field															0.37	3.64	—			
Mangpang															8.62*	—				
Bateha															—					
I Batko									11.85*	1.85	6.11	0.18	0.37	—						
Gigani									5.12	0.39	1.88	0.12	—							
Esong2									15.30*	1.48	7.45	—								
Esong1									1.90	0.45	—									
As Mundo									2.76	—										
Applat									—											
Ylig	1.14	0.10	2.51	0.12	1.02	0.85	0.26	—												
Yigo	0.44	0.01	1.80	0.94	2.74	0.24	—													
Urunao	0.04	0.22	1.01	2.15	4.48	—														
Talofofo2	5.20	1.57	7.11	0.55	—															
Talofofo1	2.63	0.45	4.53	—																
Pago	0.61	1.25	—																	
Mangilao2	0.36	—																		
Mangilao1	—																			

NOTE: The number after a site indicates first or second survey; Applat = Applatatgua.
*Significant within islands at $\alpha = 0.05$ adjusted for multiple comparisons.

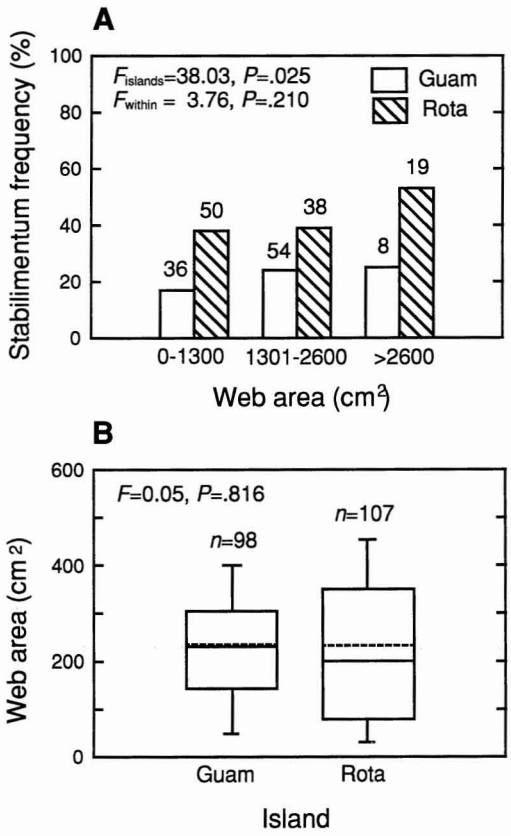

FIGURE 2. Web-area distributions of *Argiope appensa*. (A) Stabilimentum frequency in web size classes. Numbers above bars are sample sizes. (B) Tukey box plots of web-area distributions on Guam and Rota. Boxes and t-bars represent quartile ranges, dotted line indicates mean; *n*, sample size.

Islands were also generally not significant. Despite the differences in plant communities between many of the sites, within-island comparisons of sites suggested that vegetation also did not consistently influence stabilimentum frequency. Pairwise comparisons of webs from sites with identical plant communities were as likely to have significantly different stabilimentum frequencies as webs from those that had different flora (Table 1).

The lack of certain stabilimentum patterns did not contribute to the low frequency of stabilimenta on Guam. Islands having webs with the most similar frequency of occurrence of stabilimenta had proportions of stabilimentum types as different as those from islands with webs that differed most in frequency of occurrence (Table 4). As with *Argiope* spp. from New Guinea (Robinson and Robinson 1974), Panama (Robinson and Robinson 1970), Jamaica (Marples 1969), and the Galápagos Islands (Lubin 1975), diagonal stabilimenta were constructed most often in the Marianas (76.8% of the decorated webs), and tripartite and five-armed decorations were built least often (0.01%).

Stabilimentum frequencies can change greatly over time (Table 1), but probably do not account for interisland differences. The proportion of decorated webs at Esong, Rota, increased by 25.3% in 2 yr (Table 3). Conversely, the incidence of stabilimenta in webs at Laolao, Saipan, decreased by a larger margin (33.1%) in only 2 months. *Argiope* live for about 200 to 300 days (Reed et al. 1969,

TABLE 4

FREQUENCIES OF VARIATIONS IN STABILIMENTUM PATTERNS IN WEBS OF *Argiope appensa*

PATTERN	GUAM	ROTA	TINIAN	SAIPAN	TOTAL
Cross	2	2	2	9	15
Diagonal*	37	27	118	72	255
One lower arm*	9	8	6	9	33
Other†	4	9	3	12	29
Totals	55	46	129	102	332

NOTE: Categories include forms in which the pattern passes through the hub of the web.
* Left and right variants combined.
† Includes all other patterns of one to three arms and aberrant forms.

Nentwig and Heimer 1987), so the resurvey at Laolao probably included many previously censused spiders, indicating that populations of even the same individuals can vary significantly. Possible seasonal differences in decoration frequency are difficult to examine because *A. appensa* is scarce during the dry season, and I was unable to examine temporal trends between islands. However, frequencies on Guam were homogeneous (Table 3), and sites there always had a much lower proportion of decorated webs than sites from the other Mariana Islands, regardless of sampling time (Table 1).

Factors operating at scales smaller than the sample sites may influence stabilimentum frequency. Three of five sites examined in the Marianas showed significant clumping of decorated webs. Groups with decorated webs consisted of two to six spiders separated by as many as 10 undecorated webs. Because *Argiope* spp. frequently construct stabilimenta before molting (Nentwig and Heimer 1987), the nonrandom arrangment may mean that the groups consisted of sibling spiders and/or were synchronizing molts. Alternatively, *A. appensa* may be using stabilimenta as insect attractants and aggregating to increase foraging success (Craig 1991). This small-scale clumping may account for some of the variability in frequency of decorations from small samples of webs in this and other studies (Robinson and Robinson 1970, Edmunds 1986). For example, in overlapping sets of 50 adjacent webs from Obyan, Saipan, 26 to 54% of the webs had stabilimenta. Robinson and Robinson (1970) reported similar stabilimentum frequencies from Panama, ranging from 18 to 65%. This variation may be caused by their small samples (≤ 52) and the tendency of decorated webs to be clustered.

Though unlikely, the low frequency of stabilimenta in Guamanian webs could be a sampling artifact. However, recent disruption of community composition may provide an alternative explanation. As with most islands, the native communities on Guam have undergone radical changes because of the introduction of exotic organisms, extinctions of endemics, and loss of habitat (Savidge 1988, Muniappan et al. 1991). One of the most radical disruptions of any island native community has occurred on Guam, where nearly all the avifauna have been eliminated in the last 30 yr by the introduced brown tree snake, *Boiga irregularis* (Merrem) (Savidge 1987a, Conry 1988). Birds that remain are primarily migratory shorebirds, cosmopolitans, and domestic species; most forests are devoid of bird life (Savidge 1987b). Forests and second-growth habitats on other islands in the Mariana Archipelago, however, possess a largely intact native avian fauna (Conry 1988). Because birds are competitors with, and predators of, spiders, perhaps the low frequency of stabilimenta in webs on Guam is related to the avian extinctions, either directly or via possible restructuring of mutual prey communities. Birds avoid webs with stabilimenta (Horton 1980), and decorated webs survive significantly longer in the field than undecorated webs (Eisner and Nowicki 1983). If stabilimenta function as warning devices to prevent web loss from birds foraging in *Argiope* habitat (Eisner and Nowicki 1983), then perhaps the difference in decoration frequencies between Guam and the other islands is due to reduced rates of web interception. Webs represent a considerable energetic outlay for spiders (Prestwich 1977), particularly large diurnal species (Lubin 1973), and reingesting web silk at the end of a web cycle is an important part of regaining this investment (Peakall 1971). Stabilimenta, therefore, may reduce the risk of silk being lost to repeated web interceptions. In instances where flythroughs are infrequent, such as on Guam, the device may not be necessary.

If avian extinctions are prompting the low stabilimentum frequency on Guam, spiders could respond to the change in community structure in two ways. For example, a predator defense theory of stabilimentum function demands that there be an evolutionary response to the absence of birds. Because birds on Guam have only been extinct for a few decades, a rather large, but not totally improbable, selective pressure would be required to explain the low frequency on Guam. However, *Argiope* spp. are widely distributed (Levi

1983) and very good dispersers, and gene flow between adjacent archipelagic islands is probably high. Conversely, if the web advertisement or prey attractant hypotheses are correct, then decorated webs could also be an immediate behavioral response to an environmental stimulus less often experienced by Guamanian spiders.

One other study has addressed intersite variability of stabilimentum frequency. Lubin (1975) found stabilimentum frequencies in the Galápagos Archipelago similar to those reported here. *Argiope argentata* (Fabricius) webs on the island of Daphne Major were decorated 41.4% less often (Table 2) than conspecific webs from the island of Santa Cruz. Daphne Major also has fewer species of insectivorous birds (Harris 1973), which may forage in *Argiope* habitats, compete for insects, or prey on the spiders (Lubin 1975).

To summarize, stabilimentum frequency in webs of *A. appensa* was a very variable character at all scales examined in this study. The incidence of decorated webs varied significantly within and between sites, between islands, and even among a group of the same individuals. Despite this inconstancy, *A. appensa* webs on Guam maintained an unusually low frequency of stabilimenta compared with conspecific webs on adjacent islands and webs of *Argiope* spp. worldwide. The low frequency was islandwide in distribution, not correlated with web size structure of the populations, light and vegetation features, or the lack of certain stabilimentum patterns. This low incidence of stabilimenta may be a response to environmental factors peculiar to Guam, such as the massive avian extinctions that have occurred there in the last 30 yr. However, this supposition has yet to be addressed experimentally.

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